

SCHEDULE-INDUCED DEFECATION BY RATS DURING RATIO AND INTERVAL SCHEDULES OF FOOD REINFORCEMENT

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Lever pressing in rats was maintained by continuous and intermittent schedules of food while defecation was monitored. In Experiment 1, reinforcement densities were matched across variable-ratio and variable-interval schedules for three pairs of rats. Defecation occurred in all 3 rats on the variable-ratio schedule and in all 3 rats on the yoked variable-interval schedule. In Experiment 2, fixed-ratio and fixed-interval schedules with similar reinforcement densities maintained lever pressing. Defecation occurred in 3 of 4 rats on the fixed-ratio schedule and in 4 of 4 rats on the fixed-interval schedule. Almost no defecation occurred during continuous reinforcement in either experiment. These results demonstrate that defecation may occur during both ratio and interval schedules and that the inter-reinforcement interval is more important than the behavioral requirements of the schedule in generating schedule-induced defecation.

Key words: schedule-induced defecation, schedule-induced behavior, yoked schedules of reinforcement, lever press, defecation, rats

Behavior of clinical relevance—including aggression, defecation, drug self-administration, and polydipsia—can be schedule induced (Falk, 1961b; Flory, 1969; Oei & Singer, 1979; Rayfield, Segal, & Goldiamond, 1982). Such behavior occurs collaterally with schedule-controlled responding during operant schedules of reinforcement and can also occur during schedules of response-independent food delivery. If higher rates of collateral behavior occur during intermittent reinforcement than during baseline periods, the behavior may be described as *schedule induced*. Intermittent reinforcement may also serve to organize collateral behavior into patterns different than those seen during baseline, yet may not increase the overall frequency of the behavior. In this case, the behavior has been called *schedule modulated* (Wetherington & Brownstein, 1979) or *facultative* (Staddon, 1977). Several types of schedule-induced and schedule-modulated behavior have been studied in research with hu-

mans and other animals (Allen & Butler, 1990; Cross & Goodman, 1988; Davis & La Bounty, 1983; Doyle & Samson, 1988; Granger, Porter, & Christoph, 1984; Haight & Killeen, 1991; Innis, Simmelhag-Grant, & Staddon, 1983; Lucas, Timberlake, & Gawley, 1988; Mittleman, Whishaw, Jones, Kock, & Robbins, 1990; Prior, Wallace, & Milton, 1984; Riley, Wetherington, Delamater, Peele, & Dacanay, 1985; Samson & Pfeffer, 1987; Wieseler, Hanson, Chamberlain, & Thompson, 1988).

Variables influencing the development of schedule-induced behavior include interreinforcement interval (Falk, 1966), deprivation level (Falk, 1969), programmed consequences (Allen & Mathews, 1992; Pellon & Blackman, 1987, 1991), schedule history (Tang, Williams, & Falk, 1988), and the physical location of occasioning stimuli (Keehn & Jozsvai, 1990). In addition, schedule-controlled responding may interact with, and inhibit, schedule-induced behavior in determining overall rates of schedule-induced behavior (Lasiter, 1979). As such, behavioral requirements of the schedules may influence the occurrence of schedule-induced and schedule-modulated behavior. For example, polydipsia in rats occurs at lower rates during fixed-ratio (FR) relative to fixed-time (FT) reinforcement schedules of similar reinforcement density (Burks, 1970); gross movement by pigeons is reduced during fixed-interval (FI) compared to FT schedules (Osborne, 1978); and schedule-induced activity by human observers during a detection task de-

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creases during variable-interval (VI) reinforcement schedules relative to FI (Lasiter, 1979). Falk (1961a) first noted this phenomenon when reporting rates of polydipsia by rats during FR and VI schedules. Polydipsia occurred during FR schedules, but occurred at an even higher level during VI performance. In each of these instances, schedule-induced activity was more likely to occur during those reinforcement schedules that engendered lower and less consistent rates of schedule-controlled responding.

Within this context, it is interesting to examine the occurrence of schedule-induced behavior during ratio schedules of reinforcement. Schedule-induced polydipsia (Burks, 1970; Falk, 1961a) and aggression (Gentry, 1968; Gentry & Schaeffer, 1969; Huston & Desisto, 1971; Knutson, 1970) have been observed during ratio schedules. In contrast, Rayfield *et al.* (1982) reported that schedule-induced defecation by rats did not occur during FR schedules, although they did report defecation during FI, VI, and FT schedules.

Physical proximity of an occasioning stimulus is important in the development of schedule-induced behavior. For example, rats are more likely to engage in FR schedule-induced aggression when attack targets are closer (Huston & Desisto, 1971), and pigeons are more likely to engage in schedule-induced polydipsia with a water dispenser nearby (Keehn & Jozsvai, 1990). Because rats can "lever press and defecate simultaneously" (Rayfield *et al.*, 1982, p. 31), ratio contingencies should exhibit a minor influence on the development of schedule-induced defecation if interreinforcement-interval parameters are the primary determinants in the generation of schedule-induced behavior.

The present research further examines the occurrence of defecation during ratio schedules of reinforcement. In earlier research, we monitored defecation during VI and variable-ratio (VR) reinforcement schedules, but did not include those data in the final report (Wylie & Grossmann, 1988). Defecation occurred in 3 of 4 rats during VR food reinforcement schedules and in 3 of 4 rats during VI schedules. A slightly higher rate of defecation occurred for VI rats (range, three to eight boli per 15-min session) relative to VR rats (range, zero to seven boli per session), and the defecation rate decreased to zero during sessions of continuous

reinforcement. Because of discrepancies between this finding and the earlier report of Rayfield *et al.* (1982), Experiment 1 was conducted to match reinforcement density across VR and VI schedules via a yoking procedure. Experiment 2 examined defecation during FR and FI reinforcement schedules with similar reinforcement densities.

EXPERIMENT 1

Similar densities and patterns of reinforcement were programmed across ratio and interval contingencies using the yoking procedure initially described by Ferster and Skinner (1957). Six rats were grouped into three pairs. One rat of each pair responded on a VR schedule, while the other responded on a VI schedule. When a response was reinforced on the VR schedule, the next response of the rat responding on the yoked VI schedule was reinforced.

METHOD

Subjects

Six naive male Holtzman albino rats were housed individually with water freely available. The rats were selected from a group of 10, as discussed below, weighed 371 to 413 g during unrestricted feeding, and were approximately 70 days old at the beginning of the experiment. The rats were maintained at 80% ($\pm 5\%$) of their free-feeding weights throughout the experiment. Supplemental feeding was provided following experimental sessions when necessary to maintain body weights.

Apparatus

Two BRS-Foringer cubicles each housed standard operant conditioning chambers for rats (20.5 cm by 23.5 cm with a height of 19 cm). A cubicle ventilation fan and white noise presented via an internally mounted speaker masked outside sounds. A removable stainless steel pan was fitted below the grid floor (0.25 cm diameter stainless steel rods with 1.1 cm spacing between rods) of each chamber. One end panel of each chamber contained a centered feeding area (6 cm by 6 cm) and a custom-built response lever (2.75 cm by 0.5 cm) that protruded 3 cm from the end panel and was positioned 5 cm to the right of the center of the feeding area and 3 cm above the grid

floor. This translucent Plexiglas response lever could be illuminated during autoshaping by a light mounted outside the chamber and behind the lever. Bio-Serv (45-mg) food pellets were delivered by Gerbrands feeders to the feeding area. Experimental contingencies were controlled and data were collected by an Apple II+® microcomputer with a Rayfield Equipment Ltd. interface and by Gerbrands cumulative recorders.

Procedure

Daily 45-min experimental sessions occurred between the hours of 8:00 a.m. and 11:00 a.m. Defecation was monitored during schedules of food reinforcement. Immediately following each session, bolus collection pans were removed from the chambers and the chambers were examined for fecal boli that did not drop into the collection pans. Fecal boli were counted manually. Bolus collection pans were then washed and replaced.

Defecation of 10 rats was initially monitored in experimental chambers without programmed contingencies. Two alternative no-contingency baselines were arranged. During the first 13 sessions, no food was available in the feeding area. During the next phase, six 45-mg food pellets were placed in the feeding area prior to the start of each baseline session in order to acquaint the rats with the food magazine and to monitor potential changes in defecation due to the availability of food. After 6 days of this second no-contingency baseline (Sessions 14 through 19), the 6 rats with the lowest rates of defecation were selected to participate in the experiment and were matched by defecation rate into three pairs. Subsequent experimental sessions occurred simultaneously for members of each pair in the two chambers. Contingency training was implemented in Session 20 for Pairs 1 and 2. The remaining pair increased defecation during the second baseline. Consequently, a reversal to the first baseline (no food in feeding area) was programmed at the beginning of Session 22 in order to identify food as the variable responsible for the increased defecation rate. Upon reversal, there was no clear relationship between food presentation and defecation rates. Contingency training was therefore implemented in Session 35 for Pair 3.

Lever pressing was established for all rats using a free-operant acquisition procedure in

which the Plexiglas response lever was illuminated for 10 s prior to a response-independent pellet delivery. Food pellets were randomly delivered on a schedule under which the minimum interpellet interval was 30 s and the maximum interpellet interval was 90 s. The illuminated response lever darkened simultaneously with the random pellet delivery. Lever presses were reinforced on an FR 1 schedule whenever they occurred. After lever pressing was established, 1 rat from each of the three pairs was exposed to VR schedules while the second responded under yoked VI schedules. Whenever a response was reinforced on the VR schedule, a condition was arranged whereby the next response on the corresponding VI was reinforced. The VR response requirements were systematically increased over 12 sessions until a VR 100 schedule of reinforcement was in effect. Thereafter, phase changes usually were initiated after 10 consecutive sessions without increasing or decreasing trends in defecation frequency by both VR–VI partners.

The VR 100 schedule was in effect over the next 19 (Pairs 1 and 2) and 23 (Pair 3) sessions. Rates of defecation were inconsistent in Pairs 1 and 2, so the schedule requirements were increased in an attempt to produce reliable adjunctive defecation. After 20 sessions with the VR schedule set at 250, a five-session FR 1 probe was introduced. (Sessions of FR 1 were limited to five because of the large increases in body weights that occurred during 45-min FR 1 sessions.) The VR 250 schedule was then reinstated for 20 sessions.

RESULTS

Little defecation occurred prior to the establishment of lever pressing. During the initial baseline (no food in feeding area), no defecation occurred for the rats of Pairs 1 and 2. No defecation occurred for the VR rat of Pair 3, and the mean rate of defecation was 0.3 boli per session for the VI rat. No defecation occurred during the second baseline (six food pellets in feeding area) for the rats of Pair 1 and for the VI rat of Pair 2, whereas the VR rat of Pair 2 averaged 0.8 boli per session. Defecation rate for the rats of Pair 3 increased during this phase to 5.7 (VR rat) and 6.5 (VI rat). After the subsequent reversal to the baseline with no food in the feeding area (which occurred for the rats of Pair 3 only), defecation

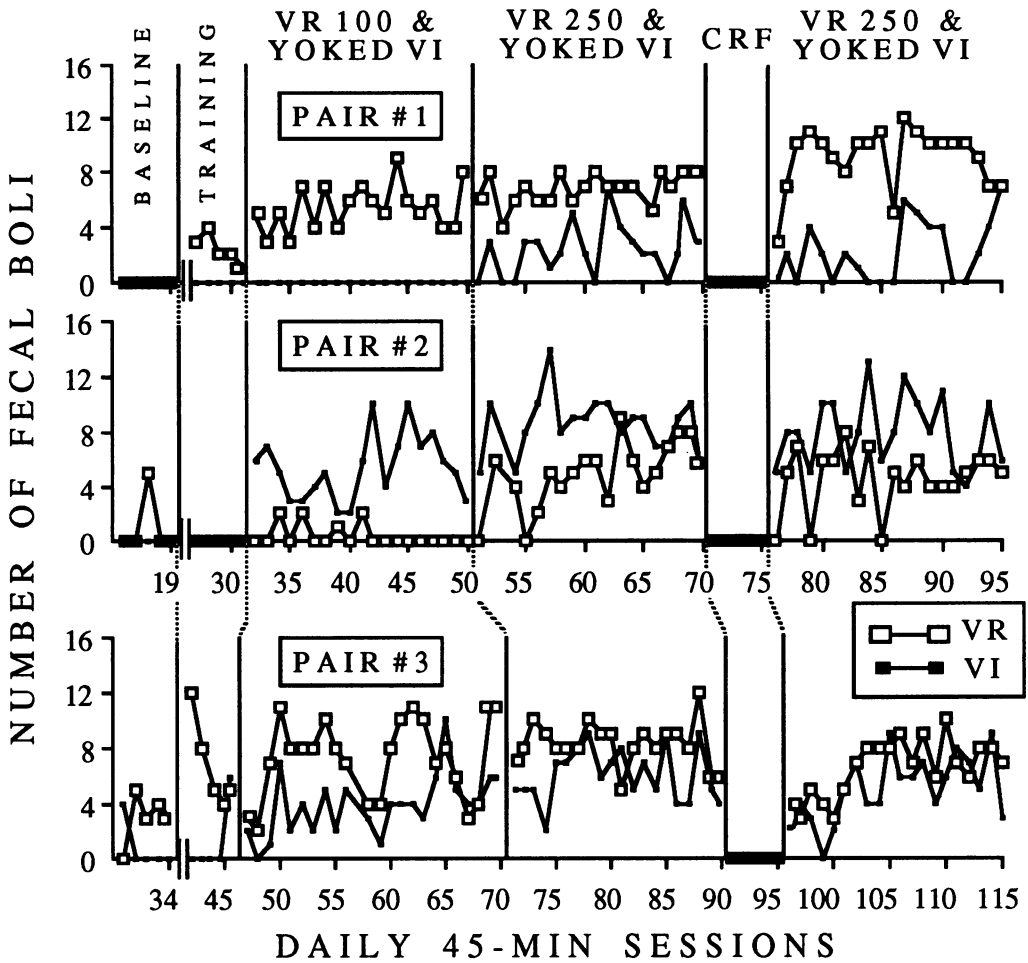


Fig. 1. Number of fecal boli dropped per session during the last five baseline sessions, the last five sessions of lever-press training, all sessions of the experimental phases in which 1 rat of each pair responded on a VR schedule and the other responded on a yoked VI, and all sessions of a phase in which the rats responded on a continuous reinforcement (CRF) schedule.

decreased to 3.4 boli per session for both rats. The mean rates of defecation during lever-press establishment and contingency training were as follows: Pair 1, 1.7 (VR rat) and 0.0 (VI rat); Pair 2, 0.8 (VR rat) and 0.3 (VI rat); Pair 3, 5.7 (VR rat) and 0.5 (VI rat).

Figure 1 shows the number of boli dropped per session during the last five baseline sessions and the last five sessions of lever-press training. For Pairs 1 and 2, the final five sessions of baseline show the phase with six food pellets in the feeding area. For Pair 3, the final five baseline sessions show the reversal phase in which no food was available. Figure 1 also

shows the frequency of defecation during all sessions of VR and yoked VI schedules and during continuous reinforcement (CRF). Defecation occurred consistently in 4 of 6 rats during the VR 100 and yoked VI schedules. When the ratio was increased to VR 250, defecation occurred in all 6 rats. Increases in defecation followed the schedule increase for 3 of 6 rats (the VI member of Pair 1 and both members of Pair 2). No rats defecated during the five sessions of FR 1. Defecation recurred when the yoked VR 250 VI contingency was reinstated. For 5 of 6 rats, rate of defecation occurred in the same range as in the initial

Table 1

The mean interreinforcement interval (in seconds) within experimental phases during VR and yoked VI schedules of reinforcement and during CRF. The interquartile range of interreinforcement intervals for each rat is also shown, and was determined by rank ordering the mean interreinforcement intervals from each daily 45-min experimental session and examining the 25th and 75th percentiles.

	VR 100		VR 250		CRF		VR 250	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Pair 1								
R1 (VR)	35	33-36	117	93-129	4	3-5	250	180-270
R2 (VI)	35	33-36	117	96-129	4	4-5	251	180-270
Pair 2								
R3 (VR)	39	38-40	111	112-117	4	3-5	133	123-142
R4 (VI)	40	38-41	111	112-117	3	3-4	133	123-142
Pair 3								
R5 (VR)	55	47-56	199	150-245	6	6-7	313	245-386
R6 (VI)	55	47-56	199	150-245	5	4-5	313	245-386

Note. The yoking procedure was not in effect during CRF. The entire range (rather than the interquartile range) is given for the CRF phase.

VR 250 phase. For 1 rat (the VR animal of Pair 1), defecation frequency increased during the final VR 250 phase.

No relationship between defecation and lever-pressing frequency could be identified in the present experiment. As expected, response frequency was higher for VR rats relative to VI rats within each yoked-contingency phase. Responding was steady during the VI schedules, and rate changes across experimental conditions were gradual. Lever-pressing rates were higher on VR 100 than on VR 250. In particular, longer postreinforcement pauses occurred on the VR 250 schedule toward the end of experimental periods, leading to a decreased overall rate. Within-run pausing was evident on cumulative records only for the VR rat of Pair 3. This pausing was brief and typically occurred late in experimental periods. During FR 1, responding was substantially and similarly decreased for all rats. When VR 250 was reintroduced following FR 1, responding similar to that occurring during the initial VR 250 recurred for the VR rats of Pairs 2 and 3, whereas a lower rate of responding occurred for the VR rat of Pair 1. Typically, many brief within-run pauses (less than 30 s) occurred, with longer pauses occurring postreinforcement. Occasionally, postreinforcement pauses lasted longer than 5 to 10 min.

Table 1 summarizes and describes the in-

terreinforcement intervals generated during this experiment. Interreinforcement intervals were similar for the members of each pair within experimental phases, suggesting that the yoking procedure adequately controlled reinforcement densities across the two reinforcement schedules.

EXPERIMENT 2

The results of Experiment 1 contrast with Rayfield et al.'s (1982) finding that defecation does not systematically occur during FR schedules. In Experiment 2, we examined defecation during FR and FI schedules of reinforcement while replicating some, but not all, of the procedures used by Rayfield et al. They observed schedule-induced defecation during FI 32-s conditions that alternated with four-session blocks of FI 1 s, but not during ascending and descending series of FR schedules. In this systematic replication, defecation of 4 rats was monitored when blocks of FR schedules alternated with blocks of continuous reinforcement. Adjusting FR schedules, as described below, were used to generate FR interreinforcement intervals of about 32 s. Defecation of 4 additional rats was monitored during alternating blocks of FI and continuous reinforcement. Reinforcement delivery for 2 of these rats was yoked to a rat on an adjusting FR to establish similar densities and patterns of reinforcement

across ratio and interval schedules of reinforcement.

METHOD

Subjects and Apparatus

Eight naive male Holtzman albino rats weighed 340 to 430 g during unrestricted feeding and were approximately 80 days old at the beginning of the experiment. As in the work by Rayfield *et al.* (1982), the rats were food deprived to 90% of their unrestricted weights prior to the start of baseline sessions, and body weights were thereafter maintained within $\pm 5\%$. Housing conditions and experimental equipment were the same as in Experiment 1.

Procedure

General procedures were the same as those described in Experiment 1 unless otherwise specified. Daily 30-min experimental sessions occurred between 10:00 a.m. and 4:00 p.m. with ratio rats and interval partners running simultaneously.

Responding of 4 arbitrarily selected rats was maintained by an FR schedule, adjusted daily to produce interreinforcement intervals of approximately 32 s. This type of schedule, referred to as an adjusting FR schedule (Ferster & Skinner, 1957), involved calculating mean interreinforcement intervals following each FR session and revising the FR requirements for the subsequent day based on trends in daily response rate. During the experiment, the adjusting FR schedule was alternated with blocks of FR 1 probe sessions.

Two different methods were used to program interreinforcement intervals of about 32 s for the other 4 rats trained with interval schedules. Responding of 2 rats (FI1 and FI2) was maintained by an FI 32-s schedule. Responding of the other 2 rats (YFI3 and YFI4) was maintained on a schedule in which reinforcers were yoked to reinforcer delivery to the rats responding on the adjusting FR schedules (Subjects AFR3 and AFR4, respectively). The yoking procedure was as described in Experiment 1. This procedure produced consistent "fixed" interreinforcement intervals to the extent that paired fixed-ratio rats responded consistently; under these conditions, schedule requirements would be expected to approximate fixed intervals rather than variable intervals.

Following the establishment of lever press-

ing by hand shaping, four sessions of FR 1 were programmed. A brief three-session training period was then undertaken, during which schedule requirements were increased daily (FR 4, 8, 16; FI 4, 8, 16 s) in preparation for the adjusting FR and FI 32-s phase. Phases of adjusting FR and FI 32 s (consisting of seven sessions each) alternated with FR 1 (four sessions) over the next 22 sessions in an ABAB design.

RESULTS

Data on the frequency of defecation during the adjusting FR and FI schedules are presented in Figures 2 and 3. To facilitate comparison with data presented in the original report, number of boli are graphed cumulatively in the format used by Rayfield *et al.* (1982). Only three instances of defecation occurred during FR 1, and these occurred immediately following phase changes to FR 1: Rat AFR2 dropped one bolus in Session 15 and two boli in Session 26, and Rat YFI3 dropped one bolus in Session 26. Defecation occurred more often when ratio and interval reinforcement schedules were introduced. Figure 2 shows that defecation occurred during the adjusting FR for 3 of 4 rats. Figure 3 shows that defecation occurred for all 4 rats on FI schedules.

Daily adjustments were made in the adjusting FR schedules. Table 2 summarizes the FR values and interreinforcement intervals during each of the two experimental phases. In general, schedules of FR 20 to FR 40 maintained responding while generating interreinforcement intervals ranging from 25 s to 40 s. No relationship between lever pressing and defecation could be identified in the present experiment. The ratio and interval schedules maintained similar rates of lever pressing, although an increasing trend in response rate was evident on the ratio schedule during the second adjusting FR phase. Similar response frequencies occurred for all rats during the three FR 1 phases, and an increasing trend in rate was evident across these three phases.

DISCUSSION

Schedule-induced defecation occurred during VR and VI schedules in Experiment 1 and adjusting FR and FI schedules in Experiment 2. Almost no defecation occurred during con-

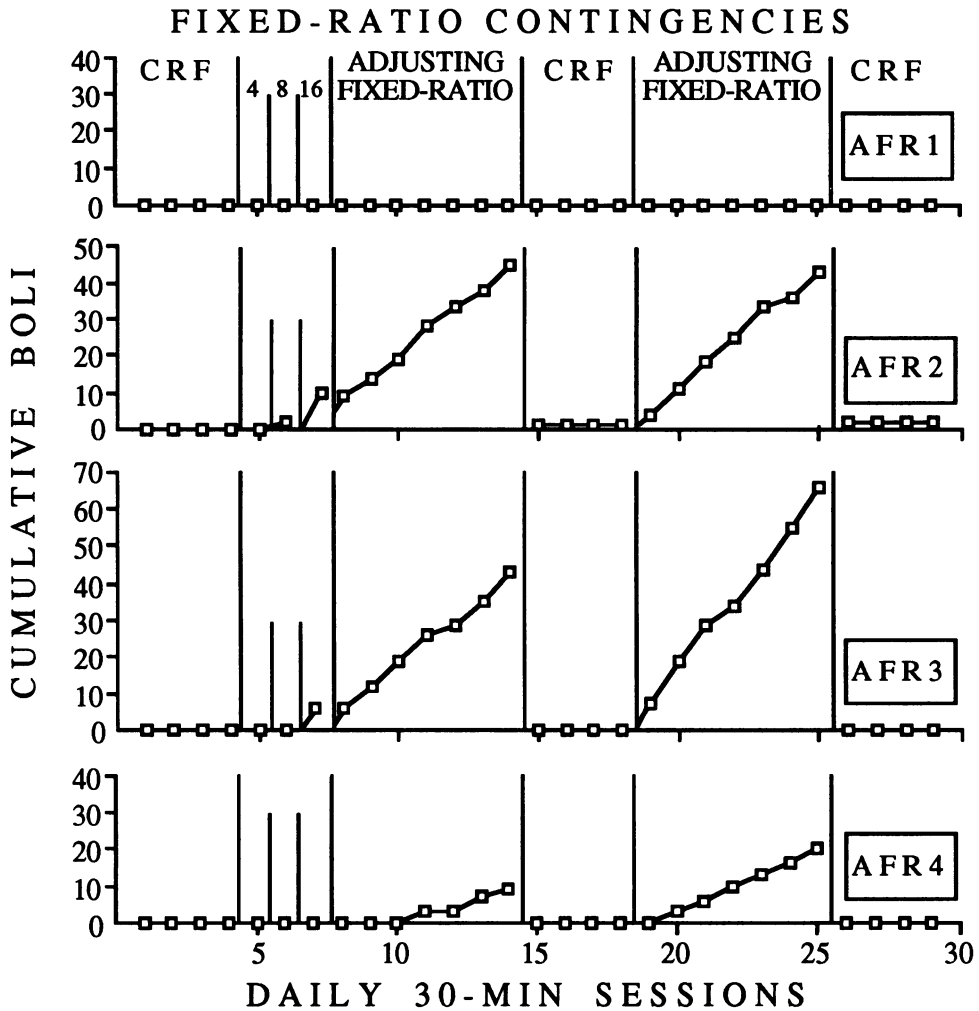


Fig. 2. Number of fecal boli dropped each session, cumulated over each experimental phase for each of 4 rats. Phases of continuous reinforcement (CRF) were alternated with phases of adjusting FR contingencies. Before the first adjusting FR phase, a three-session period was programmed in which the FR was raised from 4 to 8 to 16.

tinuous reinforcement in either experiment. These results show that defecation by rats occurs during both ratio and interval schedules of food reinforcement.

These results suggest that temporal parameters of food delivery are more important than ongoing contingency requirements in the occurrence of schedule-induced behavior. Behavioral requirements of schedules may limit, organize, or pattern schedule-induced behavior when the topographies of schedule-induced behavior are not compatible with behavior established by contingency requirements. However, this does not occur with defecation because of the opportunity for simultaneous

occurrence of defecation and lever pressing. Consequently, defecation occurs during both ratio and interval schedules of reinforcement when similar reinforcement densities are programmed across schedules. This suggests that similar rates of other types of schedule-induced behavior (e.g., polydipsia) may occur across ratio, interval, and response-independent schedules with similar reinforcement densities if opportunities for the simultaneous occurrence of schedule-controlled and schedule-induced behavior are arranged (e.g., convenient placement of a drinking spout next to a response lever). For example, Burks (1970) examined polydipsia in 4 rats during FR and

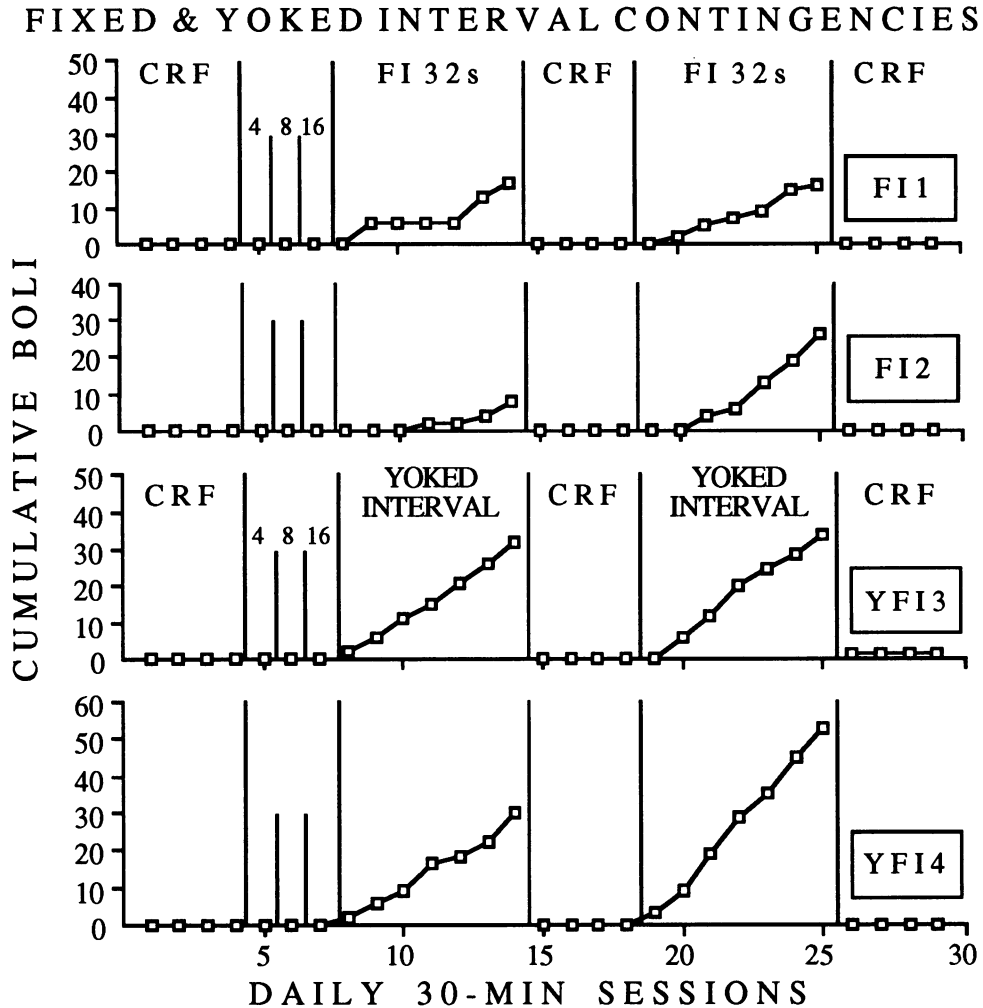


Fig. 3. Number of fecal boli dropped each session, cumulated over each experimental phase. Two subjects (FI1, FI2) were exposed to experimental phases of continuous reinforcement (CRF) alternating with FI 32-s contingencies. Two other subjects (YFI3, YFI4) were exposed to CRF alternating with interval contingencies yoked to adjusting FR contingencies. Before the first FI 32-s phase, a three-session period was programmed in which the FI was raised from 4 s to 8 s to 16 s.

FT schedules of food reinforcement with equal reinforcement densities. The positioning of the drinking tube relative to the response lever did not permit simultaneous occurrence of polydipsia and lever pressing. A slightly higher rate of polydipsia occurred during the FT schedule. Burks (1970, p. 357) suggested that this "was probably due to the removal of the bar-press requirement which increased the opportunity to drink in the FT case."

To the extent that the study of schedule-induced defecation permits the noncompetitive occurrence of defecation with schedule-controlled responding, it also provides the oppor-

tunity to examine the occurrence of defecation with other types of schedule-induced behavior. Cook, Wallace, and Singer (1983) reported excessive defecation during conditions that generated schedule-induced polydipsia, but their design did not permit analysis of the interaction of defecation and drinking. Their results do, however, suggest that polydipsia and defecation can appear concurrently. Interactions among schedule-induced behavior and schedule-modulated behavior typically have been studied by introducing and removing one or more response options, such as a running wheel or a drinking tube, that occasion mu-

tually exclusive activities (Knutson & Schrader, 1975; Roper, 1978; Yoburn & Cohen, 1979) or by using elaborate behavior coding systems in rich multiple-response environments (Innis et al., 1983; Lucas et al., 1988; Reid, Vazquez, & Rico, 1985; Riley et al., 1985). Although complex interactions among schedule-induced behavior and schedule-modulated behavior are evident in these studies, only Cook et al. (1983) reported information on the occurrence of defecation. Because we presume that defecation can occur simultaneously with most types of behavior studied in operant research, it is interesting to speculate on the interaction of schedule-induced defecation with other schedule-induced activities. In particular, has schedule-induced defecation reliably occurred in previous studies of adjunctive behavior and simply escaped notice? Or has the development of excessive defecation been precluded by the development of alternative schedule-induced activities?

Different conclusions regarding the occurrence of defecation during ratio schedules can be drawn from the present research and from the results of Rayfield et al. (1982). The VR schedules and FR 1 probe reported in Experiment 1 and the adjusting FR schedules and FR 1 probes in Experiment 2 are procedurally distinct from the ascending and descending series of FRs used by Rayfield et al. These procedural variations may account for the different outcomes, and, if so, a direct replication of Rayfield et al.'s experiment will clarify the role of procedural variables in the generation of schedule-induced defecation. An alternative explanation for these discrepant results comes from an examination of defecation prevalence rates. Rayfield et al. observed a 33% (one of three) prevalence rate of defecation during FR schedules of food reinforcement and a 94% (17 of 18) prevalence rate during FI, VI, and FT schedules of food and water reinforcement. In the present research, 6 of 7 rats defecated during ratio reinforcement schedules, and 3 of 4 rats defecated during our preliminary VR schedule study (as discussed in the introduction of this report), producing an overall prevalence rate of 82% (9 of 11). The prevalence of defecation during interval schedules of reinforcement was 91% (10 of 11), including data of 4 rats from the preliminary study. Defecation prevalence of 75% (12 of 16 rats) was reported by Wylie, Springis, and Johnson (1992) during FT schedules. These results suggest that

Table 2
Mean and range (in parentheses) of fixed-ratios presented and interreinforcement intervals (IRI) generated during the two phases with adjusting FRs.

Rat	First phase		Second phase	
	FR	IRI (s)	FR	IRI (s)
AFR1	20 (12-23)	33 (23-42)	25 (23-29)	31 (23-35)
AFR2	28 (14-39)	29 (20-38)	38 (36-40)	32 (26-39)
AFR3	23 (18-24)	37 (27-49)	24 (20-30)	39 (24-60)
AFR4	28 (22-38)	32 (26-38)	37 (36-42)	33 (28-44)

Note. Interreinforcement intervals generated by FR responding by AFR3 and AFR4 are representative of the yoked intervals presented to YFI3 and YFI4, respectively. Consistent interreinforcement intervals (approximately 32 s) were generated during presentation of the FI 32-s schedules to subjects FI1 and FI2.

not all rats defecate during conditions that typically generate schedule-induced defecation; regular differences in prevalence across rats and population sampling may explain the observed differences in ratio-induced defecation across the present report and that of Rayfield et al.

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